

A NEW FOSSIL BASKING SHARK (LAMNIFORMES: CETORHINIDAE) FROM THE MIDDLE MIOCENE SHARKTOOTH HILL BONEBED, KERN COUNTY, CALIFORNIA¹

BRUCE J. WELTON²

ABSTRACT. Isolated teeth of a middle Miocene cetorhinid genus, *Cetorhinus* Blainville 1816, occur abundantly in rocks of the Round Mountain Silt, Sharktooth Hill Bonebed, southeastern San Joaquin Valley, Kern County, California. Tooth sets of juvenile and adult dentitions of the Sharktooth Hill *Cetorhinus* were reconstructed and used as a basis for description of a new species, *C. huddlestoni*. The teeth of *C. huddlestoni* are of about the same size as those of adult *C. maximus*, the only other species of *Cetorhinus*. *Cetorhinus huddlestoni* has weak gradient monognathic heterodonty, moderate dignathic heterodonty, no disjunct monognathic heterodonty in either jaw, and strong ontogenetic heterodonty; there is presently no evidence of sexual dimorphism. Attributes noted in *C. huddlestoni* and absent in *C. maximus* include the following: bilobate roots in most adult teeth; broad based crowns with a wide, tall cusp and sharp apex in adult teeth; narrow and erect crowns in juvenile teeth; a smooth mesial and distal profile across the crown foot–root junction; mesial cusplets on some teeth from distal tooth rows in juveniles, and the sporadic occurrence of a bladelike mesial cusplet in some adult teeth; long mesial cutting ridges in adult teeth. Relative to *C. huddlestoni*, the teeth of *C. maximus* appear to be more reduced, in having narrower cusps with rounded or blunt apices in adults; much higher lingual necks; hooklike, nearly horizontal cusps in juveniles; and significantly more robust, bulbous roots, perhaps to compensate for the loss of root lobes. *Cetorhinus huddlestoni* is presently only known from the eastern North Pacific, middle Miocene Round Mountain Silt, Sharktooth Hill Bonebed, and most closely resembles *Cetorhinus* cf. *C. maximus* from the early Pliocene Sands of Kattenjijk near Kallo, Belgium.

INTRODUCTION

Fossil Cetorhinidae Gill, 1862 range from middle Eocene (Lutetian) through Recent, with occurrences in Europe, North America, Antarctica, and Asia (Cappetta, 2006, 2012; Welton, 2013a). Excluding *Pseudocetorhinus* Duffin, 1998 (Welton, 2013a), the family includes two genera: *Keasius* Welton, 2013 (Eocene to Miocene), and *Cetorhinus* Blainville, 1816 (Miocene to Recent). *Keasius taylori* Welton, 2013, is the oldest known cetorhinid, occurring in the middle Eocene of Antarctica and the late Eocene of Oregon (Cione and Ruguero, 1998; Welton, 2013a). Until recently, almost all Oligocene and early Miocene cetorhinids were referred to *C. parvus* Leriche, 1908 (Cappetta, 2012; Welton, 2013a); however, this species is now placed in the genus *Keasius* (Welton, 2013a). Middle Miocene cetorhinids are generally identified as *Cetorhinus* sp., and most late Miocene through Pleistocene basking sharks have been referred to the extant species, *C. maximus* (Cappetta, 2012; Welton, 2013a).

There are approximately four nominal extinct species of *Cetorhinus*. These include *C. duponti* (Hasse, 1882), *C. selachoides* (Hasse, 1882), and *C. auratus* (Van Beneden, 1871) from the early Pliocene of Anvers, Belgium, and *C. glauconiticus* (Noetling, 1885) from the upper Rupelian (Oligocene) of Russia. The validity of *C. glauconiticus* and *C. selachoides* is questionable (Cappetta, 2006), and both *C. duponti* and *C. auratus* are junior synonyms of *C. maximus* (Woodward, 1889; Leriche, 1908, 1921; Cappetta, 2006).

Until now *Cetorhinus* was monotypic, comprising the extant basking shark, *C. maximus* (Gunnerus, 1765) (Springer and Gilbert, 1976; Compagno, 1984, 2001). The living basking shark is coastal pelagic to oceanic with a circumglobal distribution in boreal to warm-temperate waters of the continental and insular shelves. It occurs both offshore and in shallow coastal waters and

enters enclosed bays (Compagno, 2001). In the northeastern Pacific, *Cetorhinus* ranges from the Gulf of California, northern Mexico, to the Gulf of Alaska and perhaps the Aleutian Island chain (Mecklenburg et al., 2002; Lamb and Edgell, 2010). Basking sharks are among the largest living neoselachians, exceeded only in size by the whale shark *Rhincodon typus* (Smith, 1828), attaining a maximum total length of 12.2 to 15.2 m, although generally not exceeding 9.8 m (Compagno, 2001).

The fossil record of *Cetorhinus* in the eastern north Pacific basin is not well documented and is largely unstudied. The oldest occurrences of the genus are early Miocene from the Astoria Formation of Oregon and Washington, and the Olcese Sand and lower Round Mountain Silt in the southeastern San Joaquin Valley, California (Long, 1994; Welton, 2013b). *Cetorhinus* sp. has been reported from the late Miocene (Gonzalez-Barba and Thies, 2000; Stewart, 1997; Barnes, 2008) and Pliocene (Applegate, 1978) of Baja California, Mexico, the late Miocene of California (Cappetta, 2012), and *Cetorhinus* cf. *C. maximus* occurs in the late Miocene Empire Formation of Oregon (Welton, 2013b). Most Pliocene and Pleistocene basking sharks from Oregon, California, and Baja California, Mexico, are referred to the extant species *C. maximus* (Kanakoff, 1956; Fitch, 1970; Langenwaller, 1975; Long, 1994; Huddleston and Takeuchi, 2006; Boessenecker, 2011; Welton 2013b).

The middle Miocene Sharktooth Hill Bonebed occurs within the middle Round Mountain Silt in Kern County, California (Olson, 1988). This thin, laterally widespread stratigraphic interval has yielded a remarkably diverse marine vertebrate assemblage (Sharktooth Hill Local Fauna of Wood et al., 1941) representing over one hundred species of fishes, turtles, birds, marine mammals, and terrestrial reptiles, birds, and mammals (Mitchell, 1965, 1966; Barnes, 1976; Barnes and Mitchell, 1984; Barnes, 1988). Although largely undescribed, the shark and ray assemblage includes over thirty genera, approximately two-thirds of which are sharks. Jordan and Hannibal (1923:31, pl. II, B and I, but not C–F, L–M, Q, W and CC) figured two teeth of

¹ URL: www.nhm.org/scholarlypublications

² New Mexico Museum of Natural History and Science, 1801 Mountain Road NW, Albuquerque, New Mexico 87104, USA. E-mail: weltonbj@comcast.net

Cetorhinus from the Sharktooth Hill Bonebed, under the genus *Gyrace* Jordan, 1923, a junior synonym of *Galeocerdo* Muller and Henle, 1837 (Cappetta, 1987). Other paleontologists have noted the occurrence of *Cetorhinus* at Sharktooth Hill, including Mitchell, 1965; Cappetta, 1987, 2012; Long, 1994; and Welton, 2013a, 2013b, without further study. Recent research on the dentition of juvenile and adult individuals of *C. maximus* (Herman et al., 1993; Shimada, 2002a; Welton, 2013a) has contributed significant new information on the tooth morphology and heterodonty of this species. Comparison of the dentition of *C. maximus* and the Sharktooth Hill Bonebed *Cetorhinus* clearly indicates that the latter is morphologically distinct from the extant basking shark.

The purpose of the present paper is to describe a new species of *Cetorhinus* from the Sharktooth Hill Bonebed. The species is based on a large number of isolated, unassociated teeth, representing tooth rows from interpreted mesial to distal positions in both jaws, in adult and juvenile individuals. Individual teeth, as well as reconstructed tooth sets are compared directly with juvenile and adult dentitions of the Recent basking shark, *C. maximus*, and with late Miocene and younger *Cetorhinus* teeth from California, North Carolina, the Netherlands, and Belgium.

STRATIGRAPHY, AGE, AND DEPOSITIONAL ENVIRONMENT OF THE ROUND MOUNTAIN SILT, SHARKTOOTH HILL BONEBED

The name Round Mountain Silt was first used by Diepenbrock (1933) for the upper Temblor Formation at Mount Poso Oil Field, near Bakersfield, California. Keen (1943) designated as the type section for the Round Mountain Silt, a 220-foot cored interval of diatomite, siltstone, and sand, that Diepenbrock (1933) previously described from the Ohio Oil "Glide" 1 well core (sec. 13, T. 27 S., R. 27 E.). In the type well, the formation is overlain by the Santa Margarita Formation, and rests conformably upon the Olcese Sand (Addicott, 1970). Elsewhere in the Kern River-Poso Creek area, the base of the Round Mountain Silt interfingers with the underlying Olcese Sand, and is conformably overlain by the Fruitvale Shale or truncated by the Santa Margarita or Kern River formations (Olson, 1988).

Olson (1988:fig. 11) constructed a 178.5-m (585-ft) composite stratigraphic section for the Round Mountain Silt at the Sharktooth Hill locality (sections 25, 28, 35, T. 28 S., R. 28 E.), based on subsurface logs and measured outcrops sections. The correlative diatomite section in the type Round Mountain Silt at Mount Poso Oil Field is 51 m thick in the Sharktooth Hill area (Olson, 1988:fig. 11), and 30 m above this diatomite is the Sharktooth Hill Bonebed. The stratigraphic section with the bonebed is based on Addicott's (1956:no. 379) measured section, and records a 4.5-m (15-ft) interval with vertebrate fossils (Olson, 1988). The Sharktooth Hill Bonebed condensed interval is much thinner, usually between 10 and 50 cm (Pyenson et al., 2009), and is not specifically identified in the section.

Geologic and biostratigraphic age constraints on formation of the Round Mountain Silt, Sharktooth Hill Bonebed, are illustrated in Figure 1. Foraminiferal faunas and strontium isotope data from the lower part of the Round Mountain Silt indicate that the unit is no older than Luisian on the easternmost basin margin (15.9 Ma). To the west in the subsurface, the base of the Round Mountain silt may be as old as Relizian (Olson, 1988). Higher in the section, thick diatomites underlying the Sharktooth Hill Bonebed contain diatoms of the *Denticulopsis lauta* A diatom subzone that is correlative with the early middle Miocene, early Luisian equivalent (16–15 Ma) (Barron, 1986;

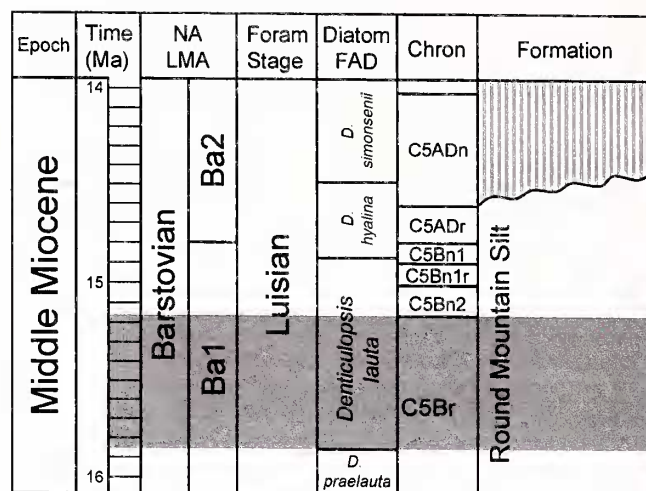


Figure 1 Geochronologic and biostratigraphic age constraints on formation of the Round Mountain Silt, Sharktooth Hill Bonebed, southeastern San Joaquin Basin, Kern County, California. Horizontal gray box defines age of bonebed formation. North American Land Mammal Ages for the Sharktooth Hill Bonebed follow Prothero et al. (2008a), Olson (1988) for the Luisian benthic foraminiferal stage, Bartow and McDougal (1984) and Olson (1988) for diatoms, and Sanchiez and Prothero (2004) for magnetic stratigraphy. Chart modified from Pyenson et al. (2009:fig. 1). Abbreviation: FAD = first appearance datum.

Olson, 1988; Pyenson et al., 2009). Data from analysis of the magnetic stratigraphy of the entire middle part of the Round Mountain Silt, including the Sharktooth Hill Bonebed (Prothero et al., 2008b) indicate the section correlates with Chron C5Br (15.2 to 16.0 Ma), and land mammals from the bonebed itself are indicative of the latest Hemingfordian to middle Barstovian, consistent with the latest early to early middle Miocene age of the formation (Liter et al., 2004; Prothero et al., 2008a). Evidence from sequence stratigraphic analysis supports deposition of the bonebed during the middle Miocene climatic optimum associated with a transgressive-regressive cycle between 16 and 15 Ma ago (Pyenson et al., 2009). The Round Mountain Silt molluscan assemblage above and below the Sharktooth Hill Bonebed contains a number of species restricted to the "Temblor" provisional provincial molluscan stage, and others that become extinct before the end of the middle Miocene (Addicott, 1970, 1972).

Silts and sandy siltstones of the lower part of the Round Mountain Silt contain foraminifers indicative of deposition at inner to outer shelf depths (Olson, 1988). Abundant foraminifers, including some species indicative of suboxic bottom conditions, occur stratigraphically higher in the section, near the base of the diatomite, and are indicative of upper Bathyal depths (Olson, 1988). The overlying massive to laminated diatomites and diatomaceous silts, containing open ocean diatoms, were deposited within this oxygen minimum zone, and between the diatomite and overlying Sharktooth Hill Bonebed, the section appears to shallow to middle and outer shelf depths (Olson, 1988).

The aerielly widespread Sharktooth Hill Bonebed, including outcrops at Natural History Museum of Los Angeles County (LACM) locality 5756, is a time-averaged accumulation (condensed section) deposited over a maximum of 700 ka, during a transgressive-regressive cycle corresponding to the middle Miocene climatic optimum (Pyenson et al., 2009).

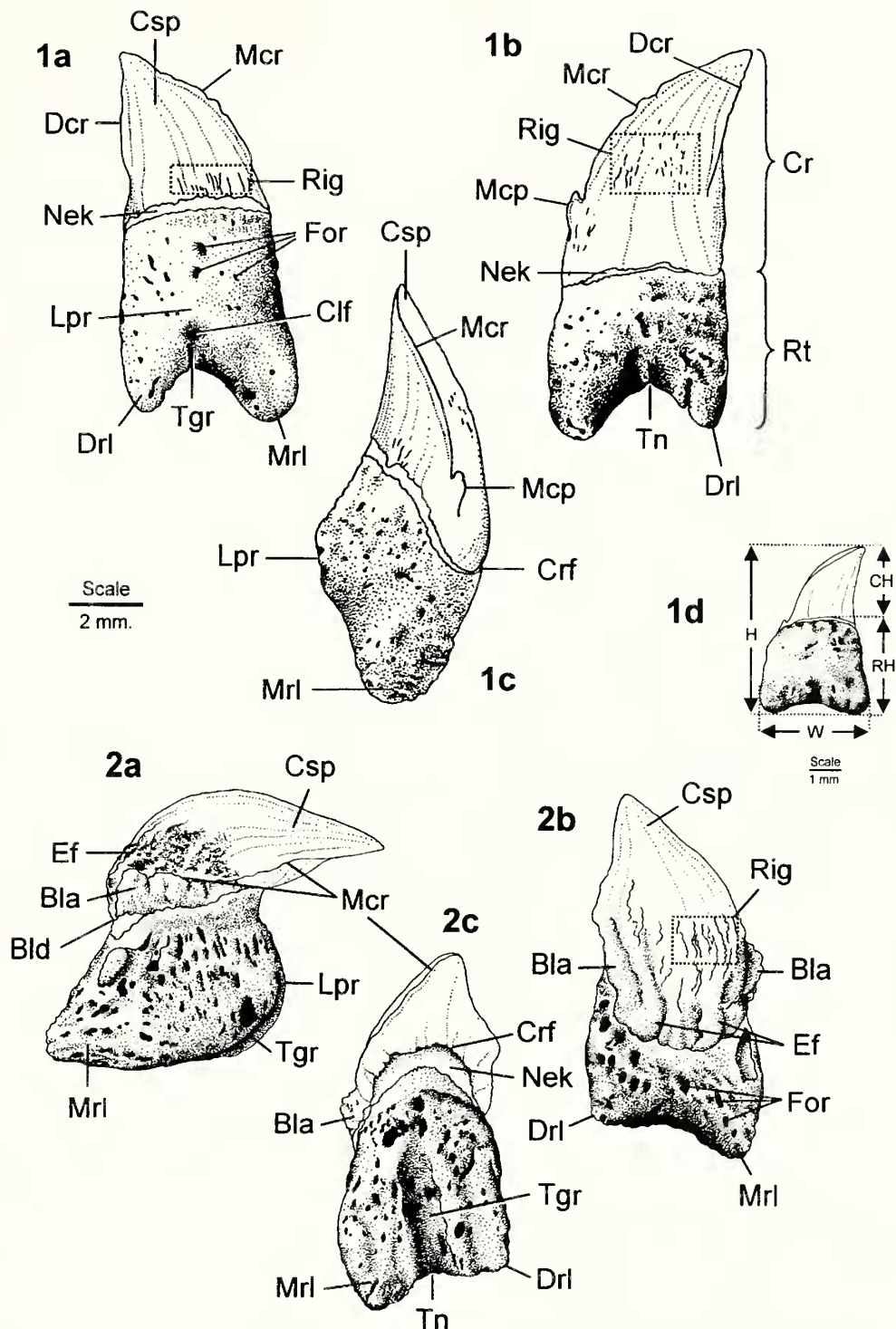


Figure 2. *Cetorhinus* tooth terminology. 1. *Cetorhinus buddlestoni*, new species, generalized tooth, modified to show mesial cusplet. 1a, Lingual view; 1b, labial view; 1c, mesial view; 1d, tooth measurements. Scale line = 2 mm for 1a-1c; scale line = 1 mm for 1d. 2. *Cetorhinus maximus*, LACM 44280-1, tooth from upper row 61, immature female, 540 cm total length. 2a, mesial view; 2b, labial view; 2c, lingual view. Scale line = 2 mm. Abbreviations: Bla = blade; Bld = basal ledge; CH = crown height; Cl = central lingual foramen; Cr = crown; Crf = crown foot; Csp = cusplet; Dcr = distal cutting ridge; Drl = distal root lobe; Ef = enameloid fold; For = foramen; H = tooth height; Lpr = lingual protuberance of root; MCP = mesial cusplet; MCR = mesial cutting ridge; Mrl = mesial root lobe; Nek = neck; Rig = ridges; RH = root height; Rt = root; Tgr = transverse groove; Tn = transverse notch; W = tooth width.

METHODS AND MATERIALS

All of the specimens described here are from the Sharktooth Hill Bonebed, and are housed in the Department of Vertebrate Paleontology, LACM, Los Angeles, California, and the Museum of Paleontology, University of California, Berkeley (UCMP). Precise locality data are on file at respective institutions.

The tooth terminology, dental homologies, and patterns of heterodonty used in this study follow, in part, Compagno (1970, 2001:15–30, and figs. 15, 16), Shimada (2002b), and Welton (2013a). The tooth terms and measurements applied to individual cetorhinid teeth are illustrated in Figure 2. All line illustrations of teeth were done by the author using a Wild M5 stereomicroscope and camera-lucida attachment. Images of some upper and lower left teeth shown in Figure 9 were reversed in order to illustrate reconstructed tooth sets of upper and lower right, juvenile and adult dentitions.

All of the Recent dentitions of *Cetorhinus maximus* described in this study are curated in the Department of Ichthyology of the LACM. The following specimens of *C. maximus* were examined: LACM 35876-1, adult male, 600–670 cm total length, wet-preserved upper and lower jaws with dentition, collected off Morro Bay, San Luis Obispo, California, 30 June 1976; LACM 44280-1, immature female, 540.6 cm total length, wet preserved upper and lower jaws, collected on Oceano Beach, San Luis Obispo County, California, 2 November 1978; LACM 39461-1, female, 635 cm total length, dried jaws with dentition, collected November 1956 from near San Pedro, California.

SYSTEMATICS

Class Chondrichthyes Huxley, 1880

Superorder Galeomorphii Compagno, 1973

Order Lamniformes Berg, 1958

Family Cetorhinidae Gill, 1862

Genus *Cetorhinus* Blainville, 1816

Cetorhinus huddlestoni, new species

Figures 3–9

Gyrace occidentalis (Agassiz, 1856); Jordan and Hannibal 1923:31, pl. II, B and I but not C–F, L–M, Q, W and CC (Cappetta, 1987:107).

Cetorhinus sp.: Mitchell, 1965:33.

Cetorhinus sp.: Cappetta, 1987:107.

Cetorhinus sp.: Long, 1994:82.

Cetorhinus sp.: Cappetta, 2012:244.

Cetorhinus sp.: Welton, 2013a:2.

Cetorhinus sp.: Welton, 2013b:76.

DIAGNOSIS OF SPECIES. A species of *Cetorhinus* that differs from *C. maximus* in having the following characters in combination: adult teeth with robust crowns, generally equal, slightly higher, or slightly lower than root height in lingual view; in mesial view, cusp apex equals or only slightly extends lingually beyond the root protuberance; mesial and distal crown margins nearly parallel, straight to convex, or slightly converging for one-half to two-thirds crown height; distal third of cusp tapers rapidly to a sharp apex; apex of cusp often with pronounced distal flexure; mesial cutting ridge generally extends from cusp apex basally for a distance of two-thirds or more of the crown height, and sometimes reaches the crown foot; cusplets generally absent, or sometimes developed above mesial crown foot as a short, labiolingually compressed blade with an apical cutting ridge that may or may not be continuous with the main mesial cutting ridge; labial crown face with highly variable, sparse to numerous, short, subparallel ridges on the upper half of the crown; enameloid folds at the labial crown foot never developed; lingual neck very narrow; in labial view, mesial and distal tooth margins not

constricted at crown foot; in mesial view, root weakly convex lingually, angular to subangular basally, and subangular to weakly convex labially; basal margin of root in lingual view usually strongly concave with short, robust, well-developed mesial and distal root lobes; lingual protuberance weakly convex and positioned high on root; a single central lingual foramen present on the lingual protuberance of many teeth; juvenile teeth with narrower, taller, more attenuated crowns; crown height in lingual view greater than root height; in mesial view, cusp apex never extends lingually beyond the root protuberance; mesial and distal crown margins nearly parallel, straight to convex, or slightly converging in lower half to one-fourth of crown; distal two-thirds to half of crown tapers to a sharp apex; cusp of some teeth are moderately twisted (axial twist) in a labial-distal direction; mesial cutting ridge generally extends from cusp apex basally for a distance of one-fourth to two-thirds cusp height, and sometimes reaches the crown foot; single mesial cusplet sometimes occurs on teeth near the distal end of the dental series in both jaws; cusplet bladelike, positioned low on crown, labiolingually compressed, and an uninterrupted mesial cutting ridge may extend across its apex; labial crown face smooth, or with sparse to numerous, short, subparallel ridges, generally on the upper half of the crown; enameloid folds at the labial crown foot never developed; lingual neck very narrow; in labial view, mesial and distal tooth margins not constricted at crown foot; in mesial view, root weakly convex lingually, angular to subangular basally, and subangular to weakly convex labially; basal margin of root in lingual view usually weakly concave to nearly flat; most teeth with weakly developed, short, mesial and distal root lobes; lingual protuberance weakly convex and positioned high on root; a single central lingual foramen is present on the lingual protuberance of some teeth.

HOLOTYPE. LACM 155726, complete lower left tooth, collected by the author in 1984.

TYPE LOCALITY. LACM locality 5756, Sharktooth Hill Bonebed, southeastern San Joaquin Valley, Round Mountain Silt, south side of Kern River, Kern River district, Kern County, California. Teeth of *Cetorhinus* collected from a thin, 20- to 30-cm-thick condensed section, containing abundant teeth and bones of marine vertebrates.

PARATYPES. LACM 155727 through LACM 155735, 9 upper adult teeth; LACM 155736 through LACM 155748, 13 lower adult teeth; LACM 155749 through LACM 155759, 11 upper juvenile teeth; LACM 155760 through LACM 155769, 10 lower juvenile teeth; LACM 155770, 1 abnormal tooth. All paratypes collected by the author in 1984 from the type locality, LACM locality 5756.

REFERRED SPECIMENS. From the upper Round Mountain Silt, Sharktooth Hill Bonebed: LACM 155771, 323 individual, unassociated teeth from the type locality, LACM locality 5756; LACM 154848 through LACM 154852, 5 teeth from LACM locality 7663; UCMP 83144, 43 teeth from UCMP locality V-6843; UCMP 98730, 70 teeth, from UCMP locality V-6843.

ETYMOLOGY. The species name, *huddlestoni*, is in honor of Mr. Richard W. Huddleston, former Curatorial Assistant, Department of Vertebrate Paleontology, LACM, who has for many years, collected, researched, and published on Neogene fishes of southern California.

RECONSTRUCTED TOOTH SETS OF CETORHINUS HUDDLESTONI. The unassociated teeth of *Cetorhinus huddlestoni*, new species, including the holotype tooth (Fig. 3), 45 paratypes (Figs. 4–8), and 323 referred teeth, were collected from a single, approximately 20- to 30-cm-thick, stratigraphic interval in the upper Round Mountain Silt, Sharktooth Hill Bonebed at LACM locality 5767. The holotype and paratypes have been used

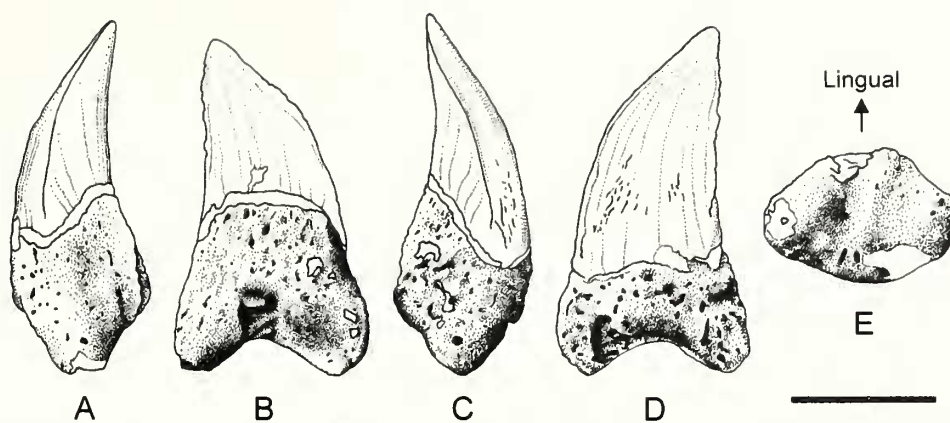


Figure 3 *Cetorhinus buddlestoni*, new species, holotype tooth, LACM 155726, LACM locality 5767, upper Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California. A, distal view; B, lingual view; C, mesial view; D, labial view; E, basal view. Scale bar = 2 mm.

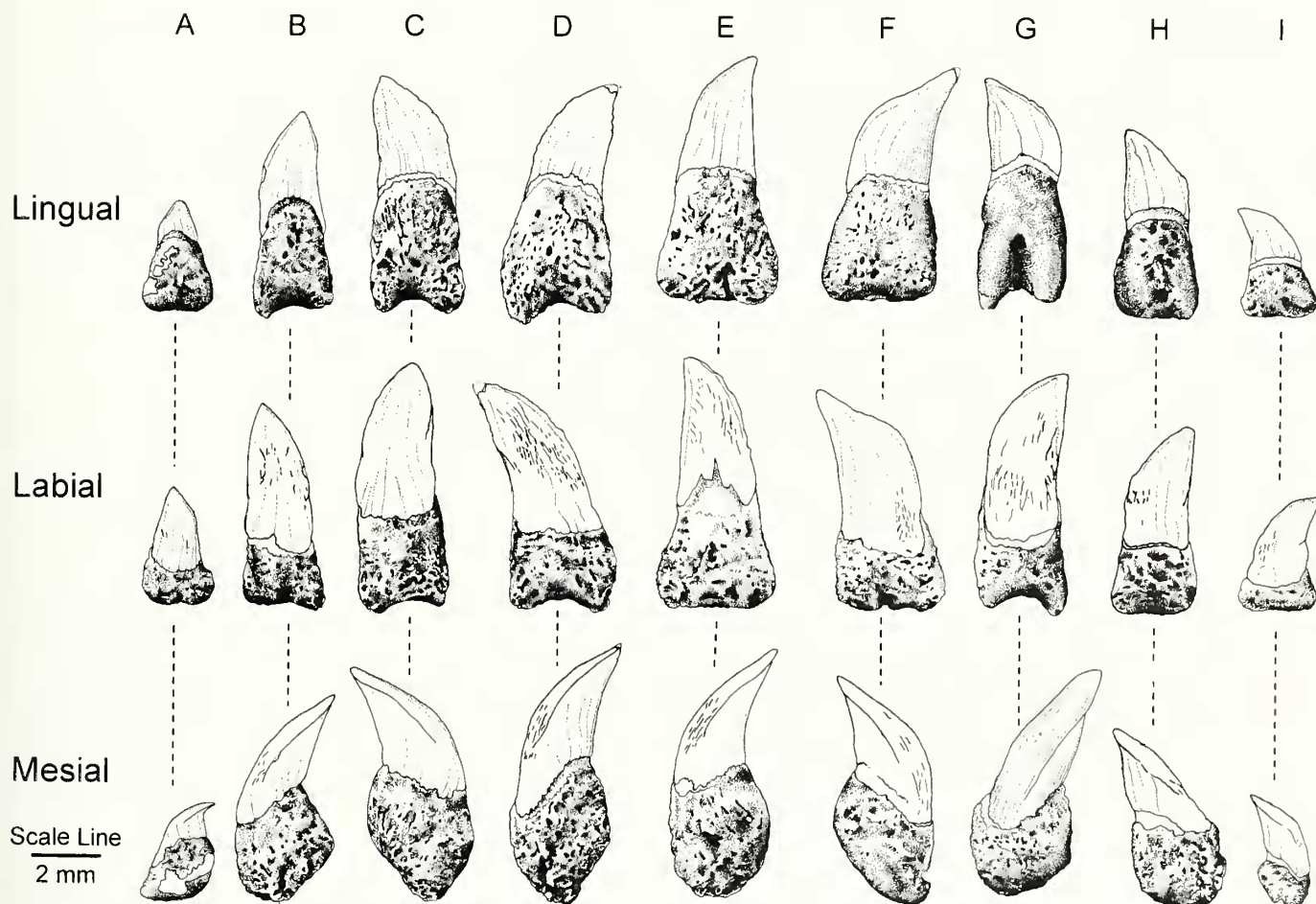


Figure 4 *Cetorhinus buddlestoni*, new species, paratypes from LACM locality 5767, middle Miocene (Barstovian), upper Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California. Hypothesized upper adult teeth, illustrated in lingual, labial, and mesial views. Teeth represent, from left to right, relative tooth row positions along the dental series, from mesial to distal. A, LACM 155727; B, LACM 155728; C, LACM 155729; D, LACM 155730; E, LACM 155731; F, LACM 155732; G, LACM 155733; H, LACM 155734; I, LACM 155735.

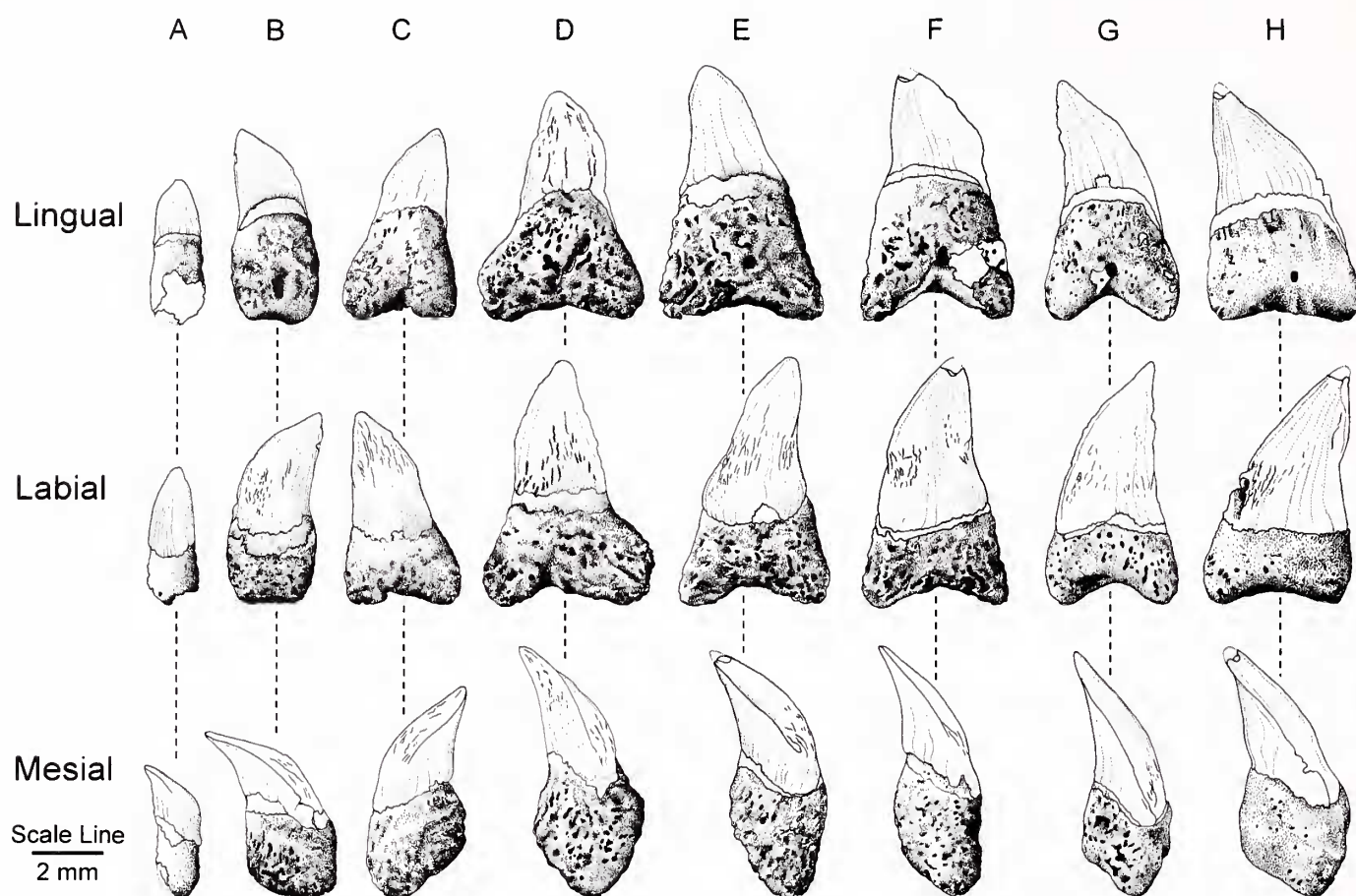


Figure 5 *Cetorbinus buddlestoni*, new species, holotype and paratypes from LACM locality 5767, middle Miocene (Barstovian), upper Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California. Hypothesized lower adult teeth, illustrated in lingual, labial, and mesial views. Teeth represent, from left to right, relative tooth row positions along the dental series, from mesial to distal. A, LACM 155736; B, LACM 155737; C, LACM 155738; D, LACM 155739; E, LACM 155740; F, LACM 155741; G, 155742. G, holotype LACM 155726.

to reconstruct tooth sets of the adult and juvenile dentitions of *C. buddlestoni* (Fig. 9). Tooth crowns are generally well preserved; however, many root surfaces are pitted and eroded, exposing porous osteodentine. Poor root preservation is a result of prolonged exposure to surface and near-surface fluids associated with formation of the condensed section, and subsequent *in situ* diagenesis.

Assignment of individual teeth to the upper and lower dental series, and to relative row positions in each jaw, is based on cusp and root morphology, and observable gradients found in the dental series of adult and juvenile *Cetorbinus maximus* (Figs. 10, 11). General attributes of the adult *C. maximus* dentition have been described by Herman et al. (1993) and Welton (2013a) and include the following: narrower and more erect crowns in the upper dentition relative to broader and somewhat shorter crowns in the lower dentition; the largest teeth in the dental series in both jaws occur approximately in the middle of the dental series; anterior teeth in either jaw have more erect crowns than those of more distal teeth; distal cusp inclination remains relatively constant along the dental series in both jaws; cusps of the lower dentition have larger teeth with broader roots than corresponding teeth in the upper dentition; the roots are more robust in teeth near the middle of the dental series in both jaws, and decrease in labiolingual width toward either end of the dental series. In

juvenile *C. maximus* teeth, crowns of the upper dentition are narrower than those of corresponding teeth in the lower dental series; lower jaw teeth are larger than corresponding teeth in the upper jaw; crowns of more mesial teeth are more erect than those more distal in the series; cusps are nearly horizontal in all juvenile teeth; the crown foot has complexly folded enameloid; mesial and distal cutting ridges are usually continuous to the crown foot, where they extend on to mesial and distal blades on some teeth.

In addition to the above attributes, there is significant variation in tooth morphology along the dental series in both jaws of *Cetorbinus buddlestoni* and *C. maximus* (Figs. 9–11), including tooth size, root width, crown shape, cusp inclination, width, and height. This variability is an attribute of the nearly homodont cetorhinid dentition. The reconstructed tooth sets (Fig. 9A, B) illustrate between 9 and 10 representative tooth positions along the dental series in each jaw. If it is assumed that *C. buddlestoni* had approximately the same number of tooth rows as *C. maximus*, then a complete artificial tooth set would require over 100 tooth rows in each jaw. The artificial tooth set is a hypothesis based on the *C. maximus* model, and constrained by the tooth morphologies present in the available sample. In the case of *C. buddlestoni*, the basic pattern of gradient heterodonty found in both jaws of *C. maximus* seems to apply for the adult dentition, and to a lesser degree, for the juvenile dentition. However, there

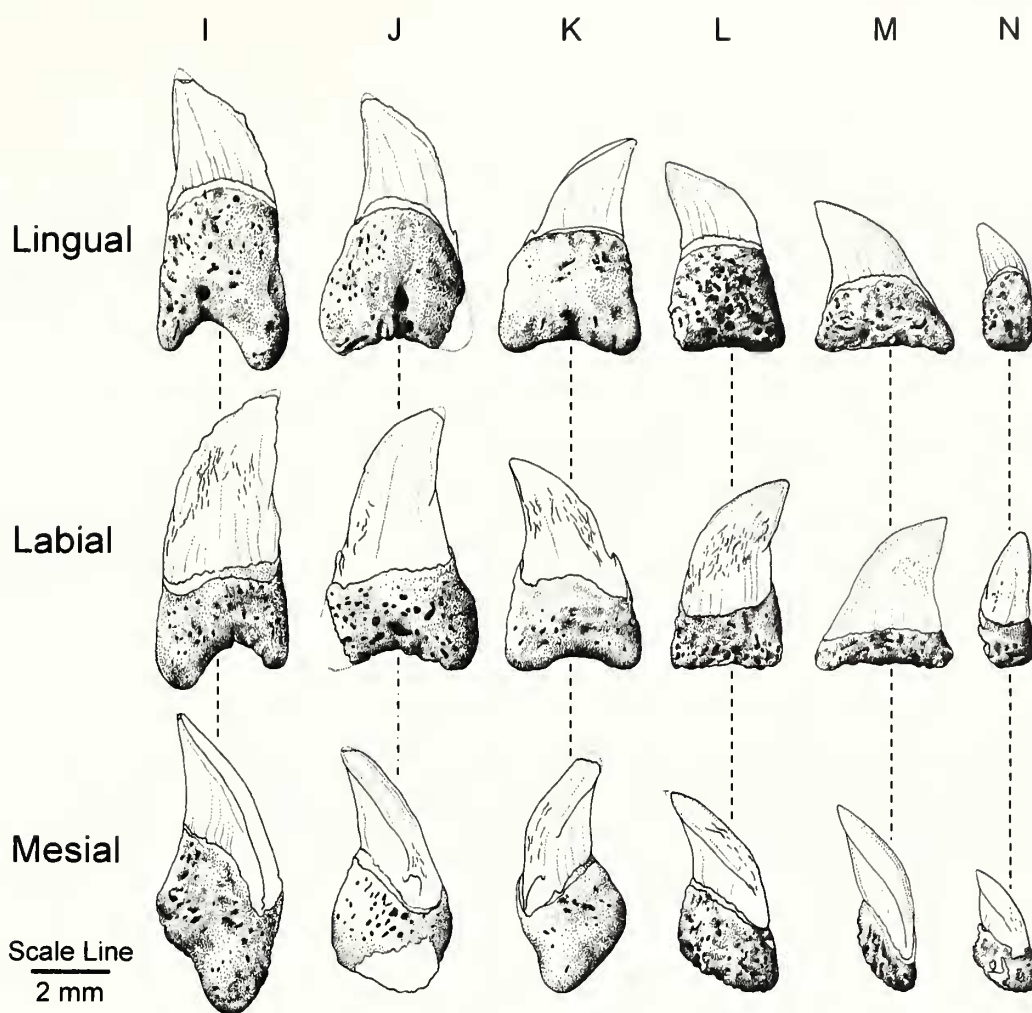


Figure 5 (continued) *Cetorhinus huddlestoni*, new species, paratypes from LACM locality 5767, middle Miocene (Barstovian), upper Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California. Hypothesized lower adult teeth, illustrated in lingual, labial, and mesial views. Teeth represent, from left to right, relative tooth row positions along the dental series, from mesial to distal. I, LACM 155743; J, LACM 155744; K, LACM 155745; L, LACM 155746; M, LACM 155747; N, LACM 155748.

are a number of significant ontogenetic differences between the dentitions of *C. maximus* and *C. huddlestoni*.

The relative ontogenetic, jaw, and row position of *Cetorhinus huddlestoni* holotype and paratype teeth have been interpreted based on the above *C. maximus* model, and used to reconstruct the tooth sets illustrated in Figure 9. The teeth illustrated in Figures 4 through 8 are grouped according to these interpretations, and described below.

DESCRIPTION OF THE HOLOTYPE. The holotype, LACM 155726 (Fig. 3A–E), is interpreted to be a lower left adult tooth, possibly from a tooth row distal to the central row in the dental series (Fig. 9A). The crown is well preserved, and the root is nearly complete, missing the tip of the distal root lobe; a small area of the root surface is broken just distal to the central lingual foramen, and lingually, a broken surface exposes osteodentine root core on the labial face of the mesial root lobe. The tooth measures 4.3 mm high and 2.7 mm wide. The crown height is slightly less than the root height lingually, and slightly greater than the root height labially. The lingual crown height in *Cetorhinus maximus* ranges from approximately equal to the

root height, to less than half the root height, depending on tooth position along the dental series (Welton, 2013a). When viewed lingually or labially, the mesial and distal tooth profile across the crown foot–root junction is uninterrupted, in contrast to most teeth of *C. maximus* where the crown root has a pronounced constriction (Figs. 10, 11). The crown is broad-based with a weakly concave distal margin and subangular mesial margin, forming a pronounced angle as it curves distally and apically. The lower half of the crown is higher, relative to most *C. maximus* adult teeth. There is no separation between crown and cusp. Unlike *C. maximus*, the cusp apex is narrow and sharp, whereas the former is often broadly rounded and blunt. The mesial and distal cutting ridges are long, extending almost to the crown foot, whereas those of *C. maximus* rarely extend two-thirds the crown height, and are usually shorter, or about half the crown height. A single, blade-like mesial cusplet occurs on some adult and juvenile teeth of *C. huddlestoni*, but are not present on the holotype. In mesial view, the cusp apex shows a slight labial recurvature, no different than *C. maximus*, but the entire crown is more erect and does not extend past the

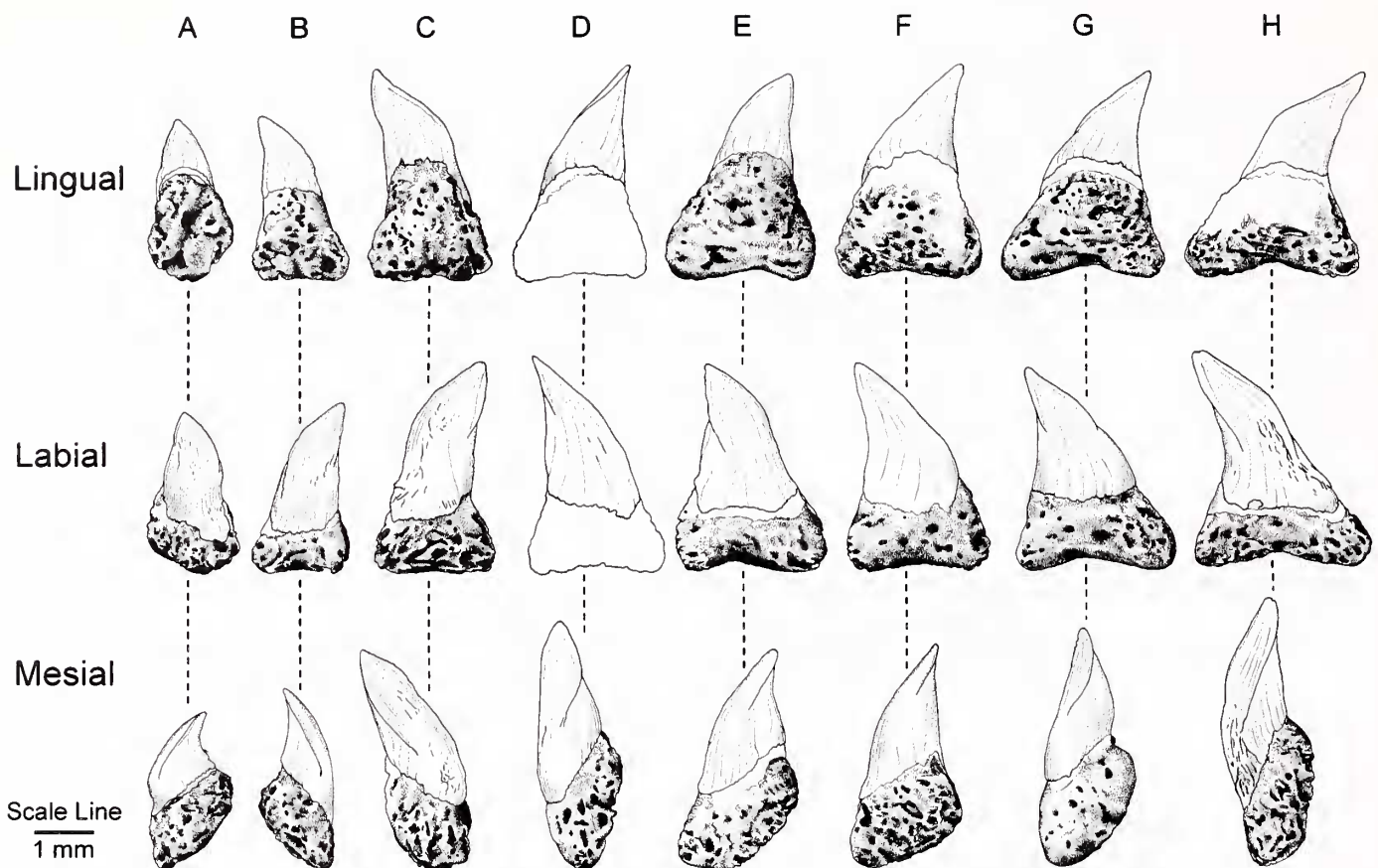


Figure 6 *Cetorhinus huddlestoni*, new species, paratypes from LACM locality 5767, middle Miocene (Barstovian), upper Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California. Hypothesized upper juvenile teeth, illustrated in lingual, labial, and mesial views. Teeth represent, from left to right, relative tooth row positions along the dental series, from mesial to distal. A, LACM 155749; B, LACM 155750; C, LACM 155751; D, LACM 155752; E, LACM 155753; F, LACM 155754; G, LACM 155755; H, 155756.

lingual margin of the lingual protuberance. The distal half of the cusp has a moderate axial twist, and the entire crown is weakly inclined distally. The lingual face is strongly convex, and smooth with no ridges. The crown foot is flat with no development of a basal ledge. The lingual neck is well developed and very wide below the midline of the crown in *C. maximus*, but weakly developed and narrow across the lingual crown foot in *C. huddlestoni*. The labial crown face is moderately convex as in *C. maximus*, with smooth enameloid and sparse small subparallel ridges about mid-crown height. The crown foot lacks a basal ledge and there are no enameloid folds or ridges as in *C. maximus*. There appears to be no development of a labial neck, or it is obscured by poor preservation. The root is wide but less robust than *C. maximus*. The lingual protuberance is less pronounced than in *C. maximus* and positioned higher on the root. The labial root margin forms a continuous convex profile with the crown, whereas in *C. maximus*, the root extends labially well past the crown foot, and is usually strongly convex. In lingual view, the basal margin is strongly embayed beneath the central foramen, forming short but well-developed mesial and distal root lobes, and root lobes are almost never developed in adult teeth of *C. maximus*. The root lobes extend beyond the crown foot mesially and distally. In contrast, the basal root margin in *C. maximus* is sometimes nearly flat, but most often strongly convex and root lobes are almost never developed.

HETERODONTY

MONOGNATHIC HETERODONTY

Monognathic heterodonty involves differences between teeth in different positions on the same jaw series (Compagno, 1970). When adjacent teeth differ strongly in morphology, the condition is termed disjunct monognathic heterodonty. Gradient monognathic heterodonty describes the condition where "a tooth in one position is different from that in another position on the same series but has a gradient of intermediate teeth between itself and the second tooth" (Compagno, 1970).

Gradient monognathic heterodonty is weakly developed in both jaws of juvenile and adults (Fig. 9A, B). In the adult male dental series (Fig. 9A) tooth size is interpreted to follow the *Cetorhinus maximus* model of an increasing size gradient from row 1 to about the midpoint of the dental series, and then gradually decreasing in size to the distal end of the dental band. The largest tooth of *C. huddlestoni* measures 8.4 mm in height. The cusps are erect at about the same angle across most of the dental series in *C. maximus*, and the teeth of *C. huddlestoni* do not vary from this model. The crowns of *C. huddlestoni*, in both the upper and lower adult dentitions (Fig. 9A), are distinctly more erect and robust than those of *C. maximus* (Fig. 10), and the cusp apices are narrower and sharper in the former, and

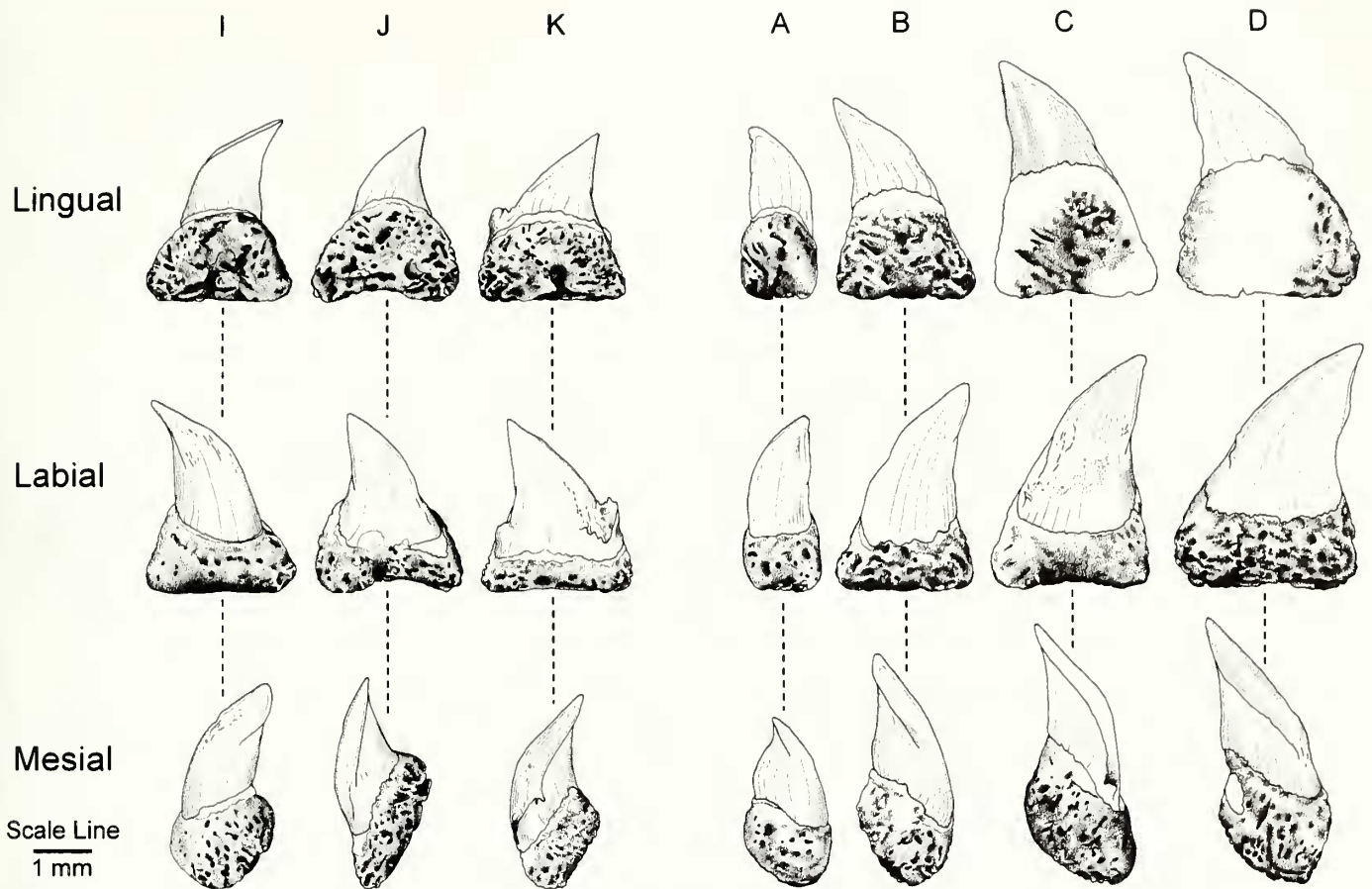


Figure 7 *Cetorhinus buddlestoni*, new species, paratypes from LACM locality 5767, middle Miocene (Barstovian), upper Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California. Hypothesized upper and lower juvenile teeth, illustrated in lingual, labial, and mesial views. I-K, continued upper juvenile dentition from Figure 6; A-D, lower juvenile dentition. Teeth represent, from left to right, relative tooth row positions along the dental series, from mesial to distal. I, LACM 155757; J, LACM 155758; K, LACM 155759; A, LACM 155760; B, LACM 155761; C, LACM 155762; D, LACM 155763.

wide and rounded in the latter. Mesial cutting ridges are generally longer than those of *C. maximus* in all tooth rows (Figs. 4, 5, 11). The lingual cusp inclination does not appear to change appreciably across the dental series, and in lingual view, there is little change in distal cusp inclination. The degree to whether this is real or an artifact of the artificial tooth set is uncertain; however, very few of the teeth in the type or referred sample have cusps with strong distal inclination. In mesial view (Fig. 11) the lingual protuberance is very pronounced in the largest adult teeth, gradually decreasing in convexity toward the mesial and distalmost tooth rows. This may also be generally true for *C. buddlestoni* (Figs. 4, 5); however, it is not as pronounced in *C. maximus* because of the weakly developed lingual protuberance in *C. buddlestoni*. Development of root lobes is apparent in both the upper and lower adult dentition of *C. buddlestoni*, and it appears that root lobes may be better developed in the more robust lower adult teeth; however, this may also be an artifact of the artificial tooth set. There does not appear to be a significant trend in the number and distribution of labial ridges on the crown face in either the upper or lower adult dentition (Figs. 4, 5) of *C. buddlestoni*. However, in *C. maximus* the ridges are generally formed about mid-crown height, whereas in *C. buddlestoni*, these ridges usually occur low

on the crown, generally just above the crown foot. Enameloid folds at the crown foot are not common in adult *C. maximus*, but absent in *C. buddlestoni*.

Disjunct monognathic heterodonty is absent in both jaws (Fig. 9). Aside from small, irregularly formed teeth adjacent to the mesial and distal ends of the dental series, there is no row-group differentiation along the dental series in either jaw.

DIGNATHIC HETERODONTY

Dignathic heterodonty, or differences in morphology between teeth in opposition or approximate opposition in the upper and lower jaws (Compagno, 1970:73) is weakly developed (Fig. 9) in *Cetorhinus maximus* (Figs. 10, 11). The most notable expression is the larger tooth size in the lower dental series relative to teeth in corresponding tooth rows in the upper dentition. In adult crowns of *C. maximus*, the cusps of upper teeth appear to be slightly more erect than corresponding teeth in the lower dentition. In the available sample of *C. buddlestoni* adult teeth, there are two populations, including higher crowned teeth with narrow roots, and lower more robust crowned teeth with wider roots. I used the *C. maximus* model to allocate the teeth to the upper and lower dental series respectively (Fig. 9).

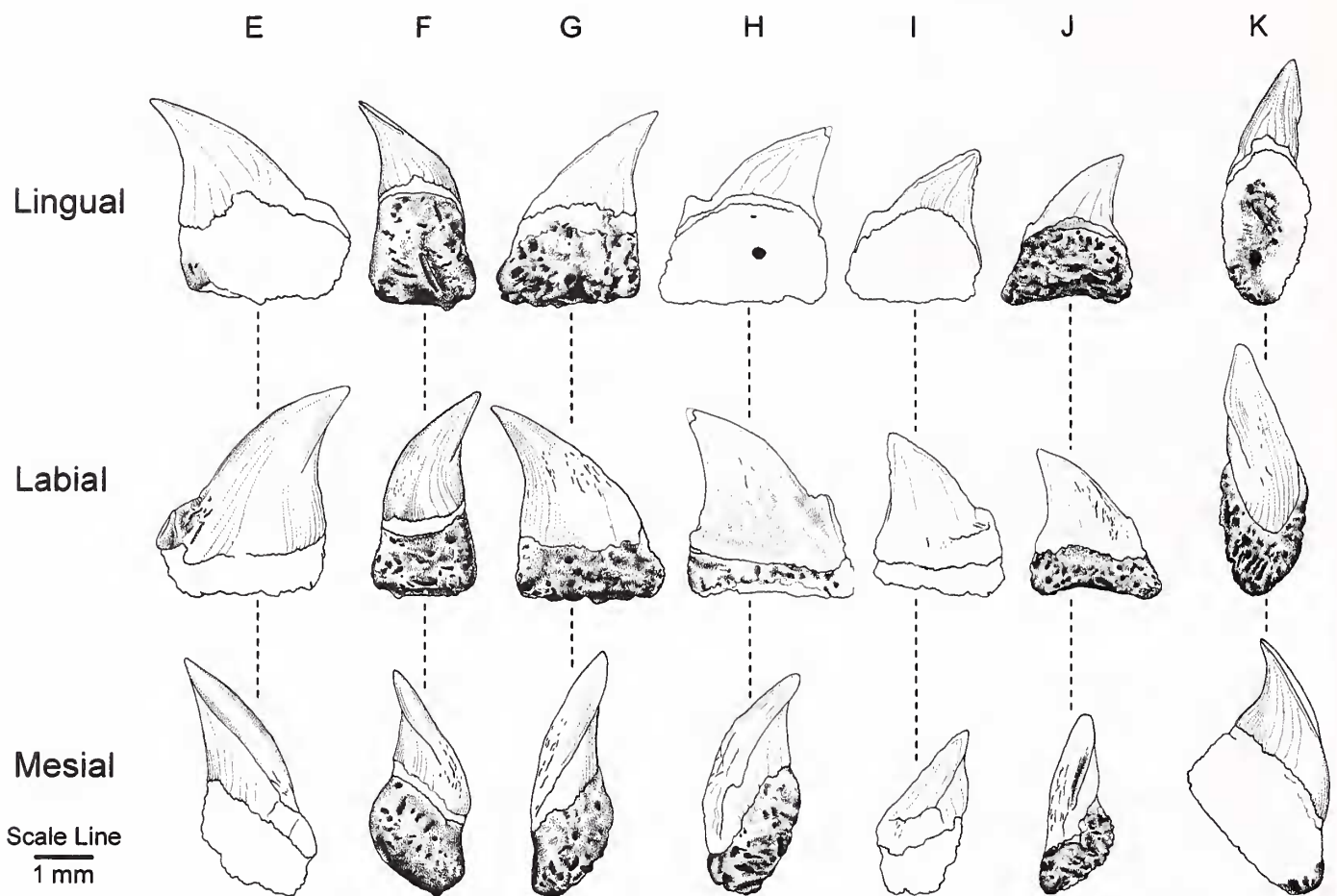


Figure 8 *Cetorhinus buddlestoni*, new species, paratypes from LACM locality 5767, middle Miocene (Barstovian), upper Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California. Hypothesized lower juvenile teeth, continued from Figure 6, illustrated in lingual, labial, and mesial views. E, LACM 155764; F, LACM 155765; G, LACM 155766; H, LACM 155767; I, LACM 155768; J, LACM 155769. K, abnormal tooth, LACM, 155770.

Compagno (2001) reported 203 to 225/225 to 230 total tooth rows for both halves of the upper and lower dentition in *Cetorhinus maximus*. Shimada (2002b:table 6) reported 100? to 131 rows for the upper dentition (row count for half the upper dentition) (200? to 262) and 100? to 139 (200? to 278 total) for the lower dentition (400? to 556 total rows). The two specimens illustrated in Figures 10 and 11 of this study have the following row counts: LACM 35876-1, 119 rows (upper right), 129 rows (lower left), and LACM 44280-1, 153 rows (upper left), and 139 rows (lower left). In macrophagous lamniforms with well-developed disjunct monognathic heterodonty, it is possible to derive reasonable estimates of row numbers from artificial tooth sets. However, in microphagous lamniforms with secondary homodonty, weak gradient monognathic heterodonty, and a high degree of morphologic variability across the dental series, it is not possible to directly establish a reasonable row number estimate from reconstructed tooth sets.

Given the similarity in tooth morphology, size, and apparently similar patterns of homodonty, it is perhaps not unreasonable to assume that *Cetorhinus buddlestoni* was of comparable size to the Recent *C. maximus*, and probably had very high tooth row counts. For this reason, I suggest in Figure 9 that the reconstructed tooth set spans ~100 or more rows.

ONTOGENETIC HETERODONTY

Ontogenetic heterodonty refers to changes in tooth morphology with growth at a functional series position in a single row or many rows (Compagno, 1970). Reconstructed tooth sets based on the smallest teeth in the *Cetorhinus buddlestoni* sample (Fig. 9B) produce upper and lower dental series that differ in many attributes from the adult dentition (Fig. 9A). It appears that, like *C. maximus* (Figs. 10, 11), *C. buddlestoni* also has strong ontogenetic heterodonty. The upper teeth of juvenile *C. buddlestoni* have narrower, more acute cusps than the adult dentition. Many of the cusps have a pronounced axial twist, and the distal cusp inclination is greater. The distal cutting ridge is shorter than the mesial cutting ridge, and the labial crown face is either smooth, or has sparse, small ridges. There are no enameloid folds at the crown foot, and mesial and distal blades are not developed. The distalmost tooth in the upper juvenile dental series (Fig. 7K) has small mesial and distal cusplets. The roots either lack mesial and distal lobes or they are weakly developed, with distal lobes being better developed in teeth of the central dental series (largest teeth) (Fig. 8B). The lower juvenile teeth have more massive, triangular crowns with strong distal inclination, and a small bladelike mesial cusplet, commonly

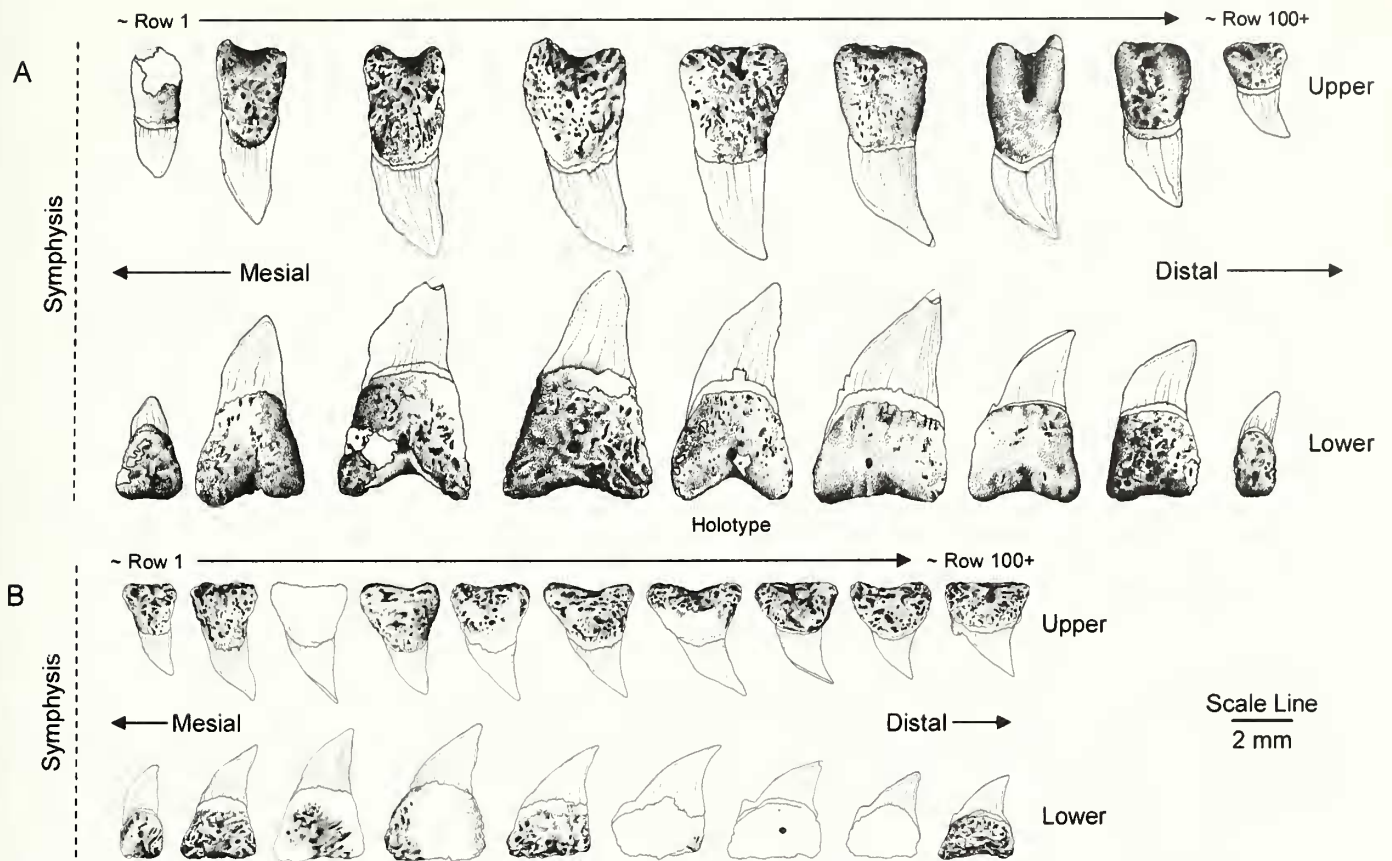


Figure 9 *Cetorhinus buddlestoni*, new species, LACM locality 5767, middle Miocene (Barstovian), Upper Round Mountain Silt, Sharktooth Hill Bonebed, Kern County, California. Reconstructed tooth sets of hypothesized upper and lower right, adult and juvenile dentitions, based on the holotype and paratypes. Individual teeth selected to represent relative row positions along the dental series in both jaws. A, adult dentition. B, juvenile dentition. See illustrations in Figures 3 through 7 for details of individual teeth. Some teeth from the left upper and lower dental series have been reversed to illustrate the right dental series. The scale line applies to both adult and juvenile dentitions.

found on the more distal tooth rows. The axial twist found in cusps of the upper juvenile dentition is not as prevalent in the lower dentition. The roots are more massive than the uppers and root lobes are not developed in most teeth. There is no difference in labial face ornamentation between the lower and upper teeth.

The juvenile teeth of *Cetorhinus buddlestoni* differ from those of *C. maximus* by the following characters in combination: cusps much more erect, as in adults of *C. buddlestoni*, and not horizontal or hook-shaped in mesial or distal view; cusps usually have an axial twist, especially in the upper dentition; lingual crown height approximately equal to root height; cusp apex does not extend lingually much past the lingual protuberance; lingual neck always narrow; lingual basal ledge absent or if present, very weakly developed; mesial cutting ridge does not reach the crown foot in most teeth, and the mesial and distal blades are never developed; mesial cusplets are occasionally developed on teeth of more distal tooth rows; crown ornamentation weak or absent; labial crown face weakly convex; constriction of teeth at crown foot–root junction absent or very weak if present; lingual protuberance moderate to weakly developed; transverse groove on lingual face of root absent.

Ontogenetic changes from juvenile to adult in *Cetorhinus buddlestoni* include the following: increase in tooth size; crowns become more massive and erect in both jaws; axial twist to cusp reduced or lost; mesial cusplets reduced or lost, although some

are retained in adult teeth; mesial and distal root lobes developed in most teeth; roots narrow in upper dentition and do not extend mesially and distally beyond the crown foot.

DENTAL SEXUAL DIMORPHISM

Dental sexual dimorphism includes “differences in morphology of teeth in approximately similar series and row positions between two individuals or groups of individuals of opposite sex and same species at about the same developmental stage” (Compagno, 1970:73). Sexual dimorphism in the dentition of *Cetorhinus maximus* is unknown (Herman et al., 1993; Welton, 2013a). If present in the dentition of *C. buddlestoni*, it would be extremely difficult to prove unless it exists in a morphologically extreme state. A clear indication of dental sexual dimorphism would be the existence of two distinct tooth morphologies for the same tooth position and stage of maturity. Proving the existence of dental sexual dimorphism in *C. buddlestoni* is unrealistic for two reasons: first, the large number of possible tooth rows, nearly homodont dentition, weak gradient heterodonty in both jaws, and variability of tooth morphology across the dental series make it extremely unlikely, if not impossible, to assign isolated unassociated fossil teeth to specific tooth rows with any credibility; and second, there is no apparent systematic trend in the teeth of *C. buddlestoni* that would suggest the presence of

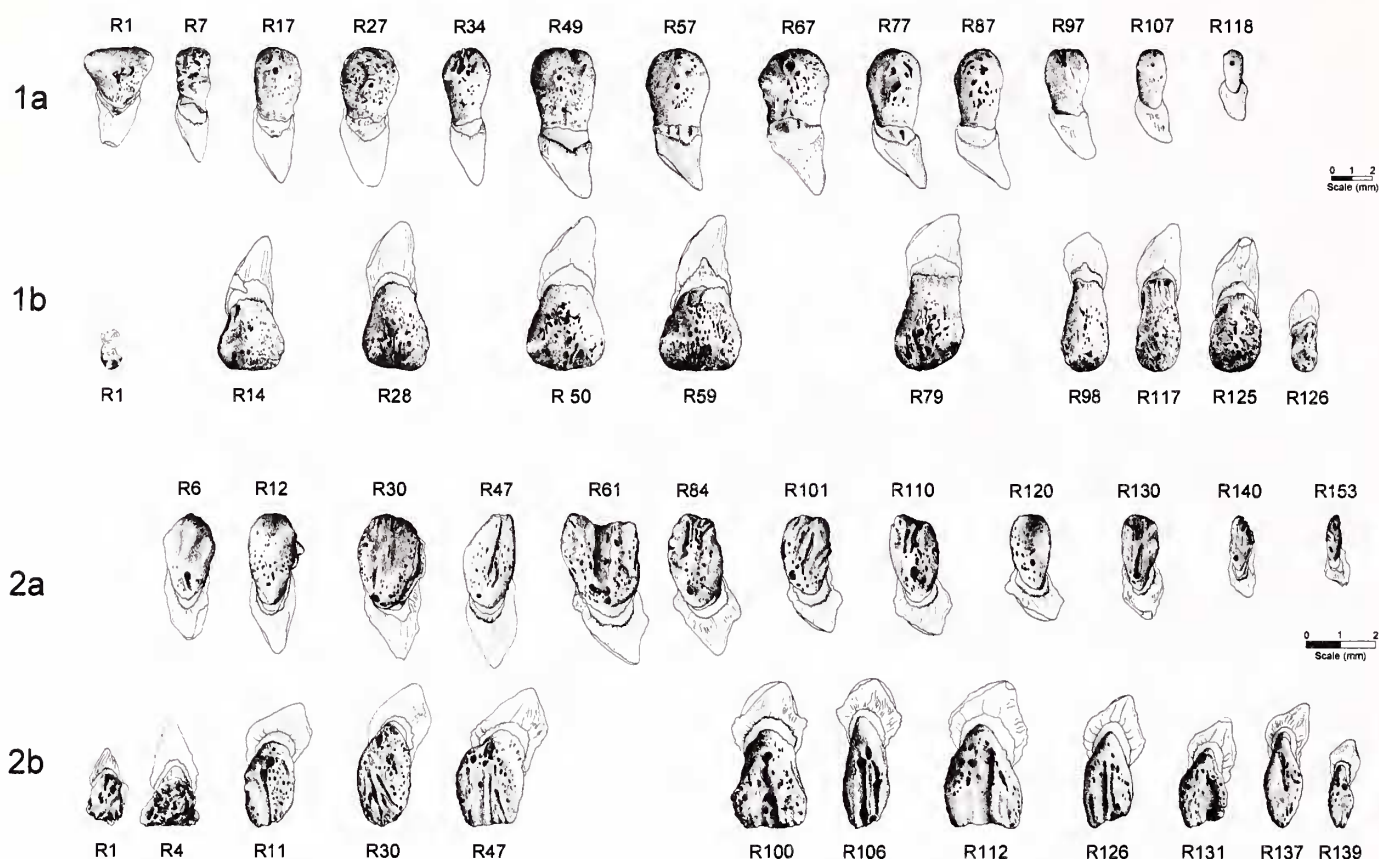


Figure 10 *Cetorhinus maximus*, upper and lower right male and female dentitions. LACM 35876-1, adult male, 600–670 cm total length, collected off Morro Bay, San Luis Obispo, California, 30 June 1976; 1a, lingual view of upper right dentition; 1b, lingual view of lower left dentition, flipped in the horizontal plane to mimic the lower right tooth series. LACM 44280-1, immature female, 540.6 cm total length, collected on Oceano Beach, San Luis Obispo County, California, 2 November 1978; 2a, lingual view of the upper left dentition, flipped in the horizontal plain to mimic the upper right tooth series; 2b, lingual view of the lower left dental series, flipped in the horizontal plain to mimic the lower right dental series. Abbreviation: R = row number. R1 at jaw symphysis.

sexual dimorphism. If it is present, but morphologically subtle, it is likely to be viewed as part of the normal dental variability found in the species.

ABNORMAL DENTITION

Shimada (2002a:fig 3) and Welton (2013a:17, fig. 9) described abnormal teeth in *Cetorhinus maximus*, including multi-cusped teeth attributed to tooth splitting, mesodistally compressed teeth occurring as isolated teeth between normal tooth rows, and row reversal. The sample of *C. buddlestoni* contains no multicusped teeth; however, two examples of laterally compressed teeth are present, one of which is illustrated in Figure 8K. Only one tooth, interpreted to be from a juvenile upper distal row, has both a mesial and distal cusplet. This might be anomalous (Fig. 7K).

DISCUSSION

The teeth of *Cetorhinus buddlestoni* are similar to an undescribed Hemingfordian *Cetorhinus* that occurs in the lower Round Mountain Silt and Olcese Sand of the southern San Joaquin Valley, Kern County, California, and coeval marine sediments from coastal Oregon. Another undescribed but slightly older

(Arikareean–Hemingfordian) and much smaller cetorhinid also occurs in the San Joaquin Basin, but appears to be more closely related to *Keasius* Welton, 2013a. The earliest occurrence of *C. maximus* is considerably younger, geochronologically, than *C. buddlestoni*, being separated in time by approximately 8 to 9 million years. At present, *C. buddlestoni* is only known from the middle Miocene (Barstovian), upper Round Mountain Silt, Sharktooth Hill Bonebed.

The adult teeth of *Cetorhinus buddlestoni* and *C. maximus* are of about the same size, and both have a nearly homodont dentition with weak gradient monognathic heterodonty, moderate dignathic heterodonty, no disjunct monognathic heterodonty in either jaw, and strong ontogenetic heterodonty. The presence of sexual dental dimorphism is unknown in *C. maximus*, and there is presently no evidence for its occurrence in *C. buddlestoni*. *Cetorhinus buddlestoni* may have had a large number of tooth rows, similar to *C. maximus*, based on similarity in adult tooth size, inferred degree of morphologic variability along the dental series, and the abundance of its teeth in the Sharktooth Hill Bonebed relative to other lamniforms.

Attributes of the teeth of *Cetorhinus buddlestoni* that are lost in *C. maximus* include bilobate roots in most adult teeth; broad-based crowns with a wide, tall cusp and sharp apex in adult teeth;

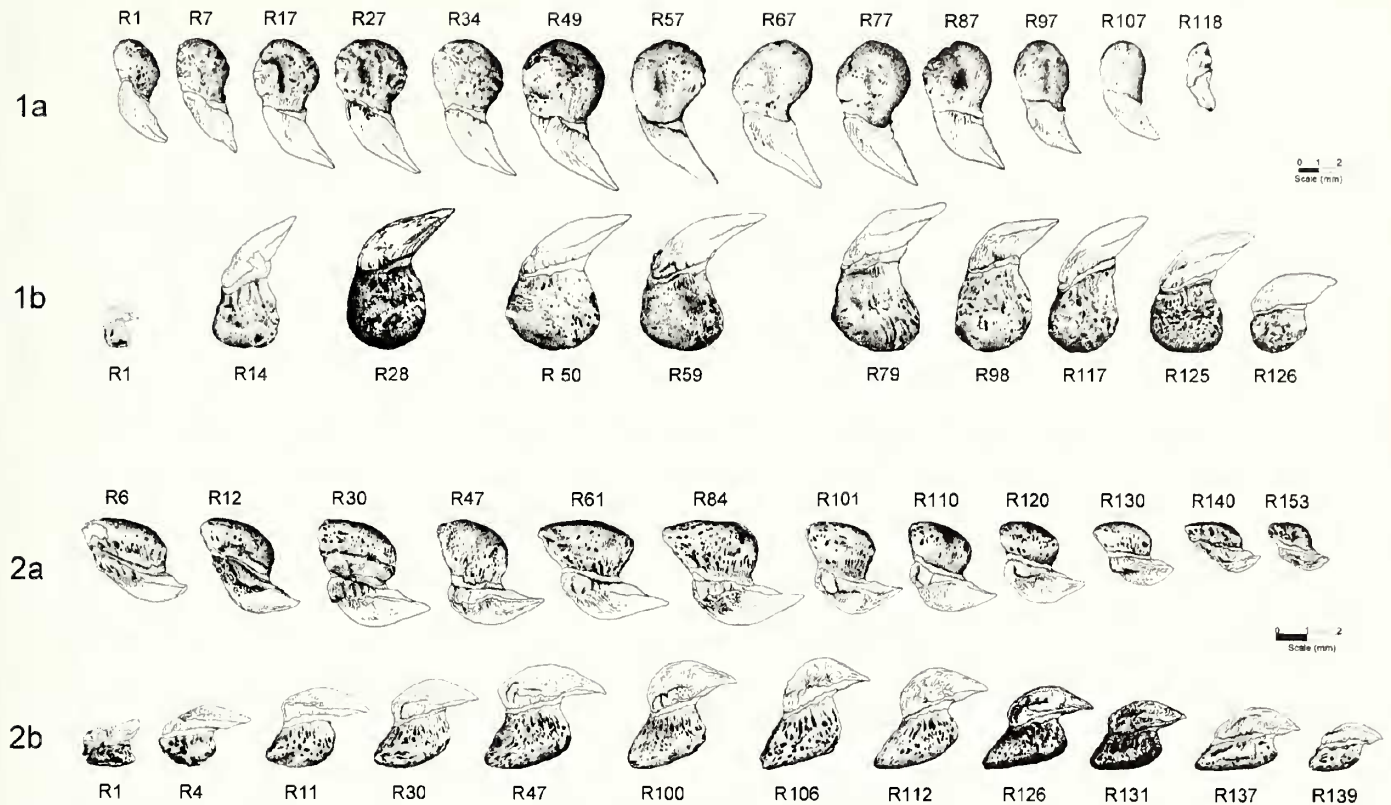


Figure 11 *Cetorhinus maximus*, upper and lower right male and female dentition. LACM 35876-1, adult male, 600–670 cm total length, collected off Morro Bay, San Luis Obispo, California, 30 June 1976; 1a, mesial view of the upper right dentition; 1b, mesial view of the lower left dentition, flipped in the horizontal plane to mimic the lower right tooth series. LACM 44280-1, immature female, 540.6 cm total length, collected on Oceano Beach, San Luis Obispo County, California, 2 November 1978; 2a, mesial view of upper left dentition, flipped in horizontal plain to mimic upper right tooth series; 2b, mesial view of lower left dental series, flipped in horizontal plain to mimic lower right dental series. Abbreviation: R = row number. R1 at jaw symphysis.

narrow and erect crowns in juvenile teeth; a smooth mesial and distal profile across the crown foot–root junction; presence of mesial cusplets on teeth from distal tooth rows in juveniles and the sporadic occurrence of a bladelike mesial cusplet in some adult teeth; and long mesial cutting ridges in adult teeth. Relative to *C. huddlestoni*, the teeth of *C. maximus* appear to be more suited to a planktivorous diet in having narrower cusps with rounded or blunt apices in adults; much higher lingual necks; hooklike, nearly horizontal cusps in juveniles; and significantly more robust, bulbous roots, perhaps to compensate for the loss of root lobes. The more robust, high crowned, sharp teeth of *C. huddlestoni* may function better for food capture during periods of gill raker shedding.

A tooth identified as *Cetorhinus* sp. from the early Miocene (Aquitainian) Pungo River Formation, Lee Creek Mine, North Carolina (Purdy et al. 2001:fig. 22c, d) is considerably older than the middle Miocene *C. huddlestoni*. Although the tooth is poorly illustrated, it appears to have a morphology closer to Pliocene–Recent *C. maximus* than to early Miocene cetorhinids or *C. huddlestoni*. It possesses a nearly horizontal, hook-shaped crown, very similar to that of a juvenile basking shark, but it lacks the extreme juvenile labial crown face ornamentation typical of modern basking sharks. The juvenile *C. maximus* tooth morphology, as described previously, is not present in the ontogeny of *C. huddlestoni*. The vertebrae figured as belonging to *Cetorhinus* (Purdy et al., 2001:108, fig. 22b) is not described in the text, and is anteroposteriorly much shorter than a typical *Cetorhinus* centrum.

In the absence of a radiograph or transverse section, which would provide details of the internal calcifications of the intermedialia, allocation of this vertebra to *Cetorhinus* is tentative.

There are no previously named middle Miocene fossil *Cetorhinus* teeth to which *C. huddlestoni* can be compared. Aside from references to the Sharktooth Hill *Cetorhinus* (Mitchell, 1965; Cappetta, 1987, 2012; Long 1994; Welton, 2013a, 2013b), all other eastern North Pacific late Miocene and younger cetorhinids are either identified as *Cetorhinus* sp. (Domning, 1978; Cappetta, 2012) or referred to *C. maximus* (Kanakoff, 1956; Fitch, 1970; Langenwaller, 1975; Long, 1994; Boessenecker, 2011; Welton, 2013b). Early Pliocene and younger cetorhinids from marine sediments of coastal California have teeth possessing most, if not all, of the dental attributes found in the Recent basking shark, and are clearly separable from those of *C. huddlestoni*. The only exception might be teeth and gill rakers identified as *C. maximus* by Boessenecker (2011) from the late Miocene or Early Pliocene Purisima Formation, north of Santa Cruz, California. Superficially, the teeth are close to *C. maximus*; however, the figures (Boessenecker, 2011:fig. 5.5–6, 5.9–14) and description do not provide sufficient detail to support this identification, and the presence of a single lateral cusplet (mesial) visible on one of the figured specimens (fig. 5–6) is an attribute generally not found in *C. maximus*.

Elsewhere, middle Miocene (Hemmoorian) teeth from the Netherlands, and referred by Van Den Bosch (1984:figs. 48, 49) to his *Cetorhinidae* Type C morphotype, are very different from

those of *Cetorhinus biddlestoni*. These teeth are more typical of undescribed early Miocene cetorhinids in having short, narrow, rounded cusps positioned on a broad crown foot, with a massive bilobate root.

Among published cetorhinids, the teeth of *C. biddlestoni* most closely resemble those from the early Pliocene Sands of Kattenjijk near Kallo, Belgium (Herman et al., 1974; Herman 1979; Van Der Bruggen, 2005). Based on figures in Herman (1979:pl. 2, figs. 1–7) these teeth share some attributes of *C. biddlestoni*, including a stocky crown with weak labial ornamentation, a strongly bilobate root, and weak or no constriction at the crown foot–root junction. However, they differ from *C. biddlestoni* in having a higher crown, apically broader cusp, blunt cusp apex, and shorter root.

CONCLUSIONS

Isolated teeth of a Middle Miocene cetorhinid genus, *Cetorhinus* Blainville 1816, occur abundantly in rocks of the Round Mountain Silt, Sharktooth Hill Bonebed, southeastern San Joaquin Valley, Kern County, California. Based on patterns of heterodonty observed in the Recent basking shark, *C. maximus* (Gunnerus, 1765), tooth sets of juvenile and adult dentitions were reconstructed, and formed the basis for description of a new species, *C. biddlestoni*. The teeth of *C. biddlestoni* are of about the same size as those of adult *C. maximus*. Both species have weak gradient monognathic heterodonty, moderate dignathic heterodonty, no disjunct monognathic heterodonty in either jaw, and strong ontogenetic heterodonty, and there is presently no evidence of sexual dimorphism in either species.

Attributes of the teeth of *Cetorhinus biddlestoni* that are not present in *C. maximus* include bilobate roots in most adult teeth, broad-based crowns with a wide, tall cusp and sharp apex in adult teeth, narrow and erect crowns in juvenile teeth, a smooth mesial and distal profile across the crown foot–root junction, presence of mesial cusplets on teeth from distal tooth rows in juveniles, the sporadic occurrence of a blade-like mesial cusplet in some adult teeth, and long mesial cutting ridges in adult teeth. Relative to *C. biddlestoni*, the teeth of *C. maximus* appear to be more reduced, in having narrower cusps with rounded or blunt apices in adults; much higher lingual necks; hook-like, nearly horizontal cusps in juveniles; and significantly more robust, bulbous roots, perhaps to compensate for the loss of root lobes.

The earliest occurrence of *Cetorhinus maximus*, the only other species of *Cetorhinus*, is considerably younger, geochronologically, than *C. biddlestoni*, being separated in time by approximately 8 to 9 million years. At present, *C. biddlestoni* is only known from the eastern North Pacific, middle Miocene Round Mountain Silt, Sharktooth Hill Bonebed. Among published cetorhinids, the teeth of *C. biddlestoni* most closely resemble those from the early Pliocene Sands of Kattenjijk near Kallo, Belgium (Herman et al., 1974; Herman, 1979; Van Der Bruggen, 2005).

ACKNOWLEDGMENTS

This study is derived from research I conducted while working on my Ph.D. dissertation at the University of California at Berkeley. I acknowledge the assistance and guidance I received from the late Joseph T. Gregory, and thank J. Howard Hutchison and Leonard J.V. Compagno for their advice and comments during my studies. I thank Samuel McLeod, Vanessa Rhue, Jeff Seigel, and Rick Feeney of the Natural History Museum of Los Angeles County, California, for providing access to specimens loaned for this study. For access to research facilities and collections, I also thank Spencer Lucas and Justin Spielmann, New Mexico Museum of Natural History and Science. Jürgen

Pollerspöck, Douglas Long, Kenshu Shimada, and Jorge Domingo Carrillo Briceño provided important literature used in this study. I thank Camm C. Swift and an anonymous reviewer for constructive criticisms of the manuscript.

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Received 19 November 2012; accepted 10 January 2014.